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RESEARCH ARTICLE

Ecological separation by ecomorphology and swimming performance between two congeneric fish species

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ABSTRACT. The high diversity of freshwater fish species reflects a great morphological plasticity. Understanding the relationship between swimming capacity, morphology and habitat use may be important to predict the chances of finding a species at an anthropized environment. The swimming capacity and morphological aspects of two sympatric species of *Characidium*, and for which spatial segregation in different hydraulic habitats is known, were compared in this study. Twenty-one individuals of *Characidium fasciatum* Reinhardt, 1867 and 23 individuals of *Characidium* cf. *zebra* Eigenmann, 1909 were captured and used for the evaluation of the swimming capacity and ecomorphological attributes. The swimming capacity of each species was obtained by measuring critical and relative velocities. A total of 12 ecomorphological attributes correlated with habitat use and swimming characteristics were also compared. The Mann-Whitney mean test showed that the swimming capacity of *C. fasciatum* was greater than that of *C.* cf. *zebra,* and the standard length of the individuals explained 12.42% of the variation in their capacity to withstand water flow. Both species were morphologically distinct in the relative length of the caudal peduncle, ventral flattening index and the relative area of the pectoral fin. The relative area of the pectoral fin alone accounted for 16.71% of the differences in the ability to resist the water flow and which were not explained by body length. Our results showed that two species differed in the ecomorphological space and in their swimming capacity, supporting the hypothesis that the greater the hydrodynamism, the better a fish is able to withstand the water flow, and that this capacity is correlated with the morphological characteristics linked to the swimming activity of the fish.

KEY WORDS. *Characidium*, environmental pressure, habitat use, intraspecific differences, morphology

INTRODUCTION

Freshwater environments harbor an estimated 12,000 species of strictly freshwater fish (Nelson 2006). The great diversity of species is reflected in a variety of reproductive behaviors, morphological plasticity, trophic plasticity and sensitivity to various environments (Gatz 1979a, Wootton 1991, Vazzoler 1996, Luiz et al. 1998, Collen et al. 2014). Knowing the biology of fish species, their ecological relationships, and their different responses to biotic and abiotic variations is necessary to understand and to mitigate the impacts of anthropic actions. Anthropic changes often degrade the environment, causing homogenization of the aquatic physical environments and loss of habitat (Lowe-McConnell 1975, Miller 1984, Jackson et al. 2001, Rosenfeld 2003, Chapman et al. 2014).

Ecological morphology, or ecomorphology, is the branch of ecology that studies the relationships between morphology and ecological aspects among individuals, populations, guilds, and communities (Karr and James 1975, Gatz 1979b, Winemiller 1992, Chapman et al. 2015). For a long time, ecologists have been interested in the relationship between the morphology of organisms, their ecological performance and the evolutionary consequences of this relationship for the selection and maintenances of adaptative traits in populations (Gatz 1979a, Wikramanayake 1990, Winemiller 1991, Leal et al. 2011, Saraiva and Pompeu 2016). Ecomorphological studies of fish aim to understand the importance of certain attributes in the ecology of the species and how they influence their adaptation to different habitats (Douglas and Matthews 1992, Norton et al. 1995, Casatti and Castro 2006, Lailvaux and Husak 2014).

The first studies on the swimming capacity of fish focused mainly on physiological aspects and how it is influenced by water characteristics such as dissolved oxygen, temperature and pH (Brett 1964). In Brazil, investigations have been generally descriptive and comparisons have been made with species from other countries (Santos et al. 2008), focusing on establishing constructive parameters for fish ladders (Santos et al. 2012). Even today, studies that experimentally test the correlation between swimming capacity and morphological aspects and/or species ecology are rare for Neotropical species (Sampaio et al. 2012). The few studies that have advanced in this direction have attempted to understand how morphological attributes possibly associated with swimming influence the use of the hydraulic habitat by a species (Casatti et al. 2001, Chapman et al. 2015).

In the present study, we compared the swimming capacity and morphological aspects of two congeneric sympatric species for which spatial segregation in different hydraulic habitats is known (Leal et al. 2011). Three hypotheses were tested: (i) the species occurring in environments with faster water velocity has greater swimming capacity; (ii) the two species differ with respect to some morphological parameters; (iii) the morphological parameters that differentiate the species are correlated with their swimming performance and explain intraspecific differences in their ability to remain positioned on the substrate despite the flow.

MATERIAL AND METHODS

Fish collecting

Individuals of the two species were collected in the Curimataí river (17°59'33.3"S; 44°10'48.2"W), São Francisco river basin, Minas Gerais, Brazil. Fish were captured with a seine and semicircular hand nets (mosquito screen with 1 mm mesh, 80 cm in diameter). The collecting points were chosen based on a previous study of the fish community of this river, which identified that two species of *Characidium* use distinct habitats (Leal et al. 2011). *Characidium* sp. cf. *Characidium zebra* Eigenmann, 1909, referred to as *Characidium* cf. *zebra* in the rest of this text, are abundant in deeper waters where the flow is low (pools) and the substrate is sandy. *Characidium fasciatum* Reinhardt, 1867 are found in rapids (riffle), where it is shallower and the substrate is rocky. In total, 21 individuals of *C. fasciatum* and 23 individuals of *C.* cf. *zebra* were captured and evaluated for their swimming capacity and ecomorphology.

After being collected, the fish were transported in aerated boxes to the experimental area, where they were placed in aquariums and left resting for 24 hours before the tests started. No fish remained in the laboratory for more than seven days, and during the experiments they were fed commercial aquarium fish food. Individuals of *C.* cf. *zebra* were maintained at average temperature of 19 °C, dissolved oxygen of 8 ppm and 9.5 of pH; *C. fasciatum* were maintained at 21.6 °C, oxygen concentration of 7.99 ppm and pH 9.5. After the tests were carried out, the fish were fixed in 10% formaldehyde solution and then stored in 70% alcohol. Individuals of both species were deposited in the Museu de Zoologia da Universidade de São Paulo (*C. zebra* MZUSP 73689 and *C. fasciatum* MZUSP 73790).

Swimming performance

The hydraulic apparatus used to perform the tests in this study consists of a hydrodynamic tunnel through which water is forced by a centrifugal pump (Sampaio et al. 2012). The tunnel is made of PVC pipes (with internal diameters of 100 mm), flexible tubes (100 mm internal diameter) and transparent acrylic tube (90 mm internal diameter and 1.0 m long). The centrifugal pump (Weg, 7.5 HP and maximum flow of 27.5 $m^3 \times h^{-1}$) promotes the flow of water, which is measured by an electronic flow meter, and controlled by a frequency inverter. A water tank (500 L) and supporting structures (in metalon, with 1.0 m height and lengths of 1.0 and 3.5 m) complete the apparatus (Fig. 1).

To determine fish swimming ability, the initial speed of the test, 0.05 $m \times s^{-1}$, was increased at a fixed rate (also 0.05 $m \times s^{-1}$) every five minutes. This interval, adopted according to Santos (2007), makes it possible to implement and measure all speeds and to complete the test within a feasible time. The test ended when the fish could no longer remain in the flow (due to muscle fatigue) and was drawn by the water flow to the downstream screen of the acrylic section (Hammer 1995). After completion of the test, the pump was shut down and then the time and the speed supported by the fish were noted. Afterwards, the critical velocity values were calculated according to Brett (1964): $V_{crit} = V_{max} + \overset{\curvearrowright}{T}_{max}/DT \# DV^{\vee}$, where Vmax is the maximum speed, Tmax the time during which the fish swam in the last time interval, ΔT the time interval and ΔV the speed increment. The relative velocity, in lengths per second, was also obtained by dividing the critical velocity value by the length of each fish, in order to allow comparisons between individuals by removing possible size effects.

A linear regression was also performed to evaluate the influence of body size on the critical velocity, and the data were transformed (Log10) when the values did not have a normal distribution. The Wilcoxon-Mann-Whitney test was used to compare the relative velocities between species.

The individuals of both species of *Characidum* were considered unsteady swimmers (Langerhans 2009): they resist the flow of water, standing still on the substrate. Therefore, when we refer to swimming capacity this fish it may mean that it is both actively swimming and/or resisting the flow of water.

Ecomorphology

Morphometric measurements were performed on all individuals for which we evaluated the swimming capacity, using a digital caliper with an accuracy of 0.01 mm. All measurements were taken on the left side of each fish. The body area, caudal fin and pectoral fin were measured from drawings made on graph paper. Eighteen measurements were used, including

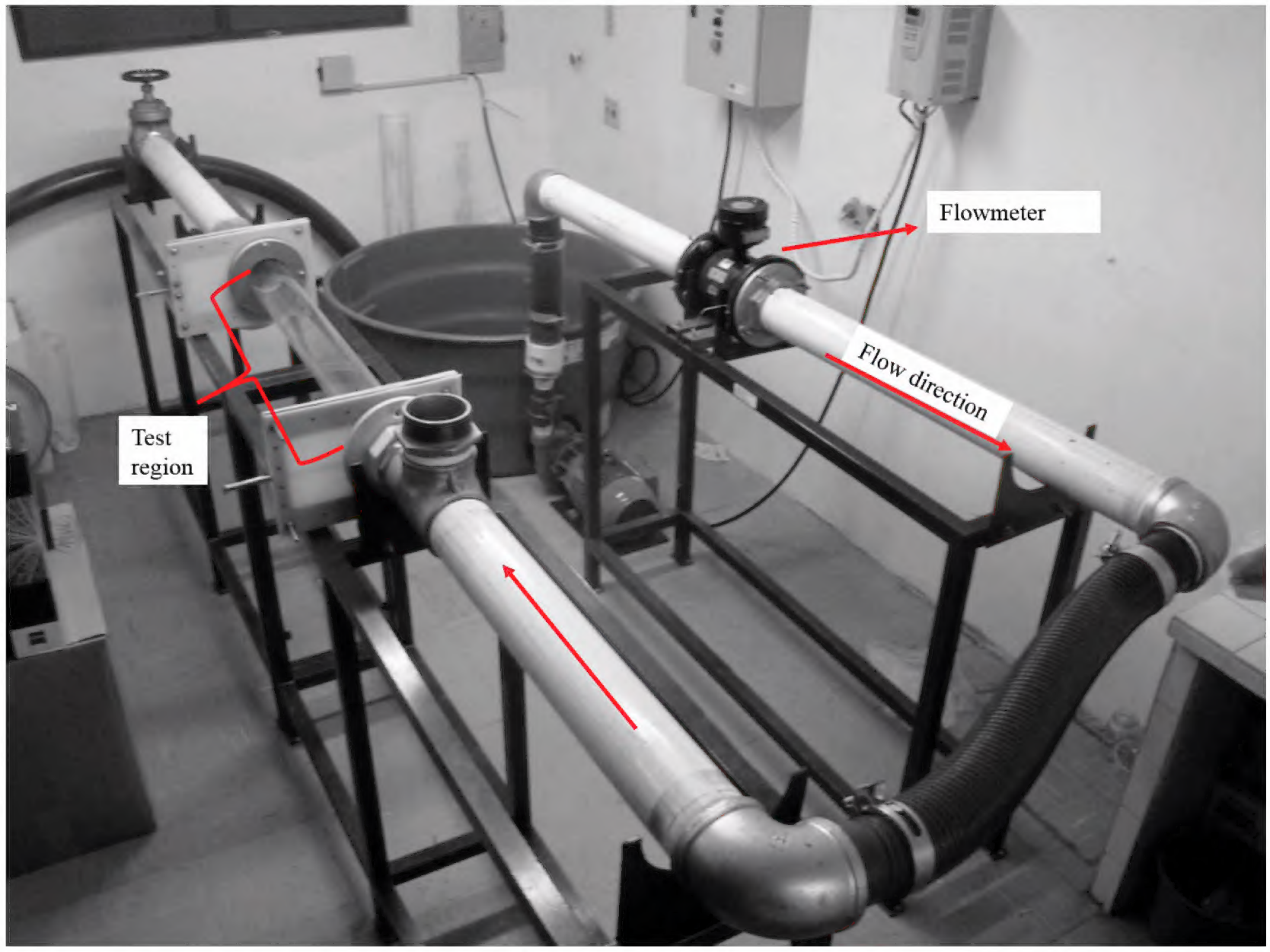


Figure 1. Experimental apparatus of swimming capacity showing the test region and flow direction.

linear and area measurements, which were converted into 12 ecomorphological attributes, correlated with both habitat use and swimming characteristics: (CI) Compression index: High indexes indicate laterally compressed fish that live in lentic ecosystems (Watson and Balon 1984). (RH) Relative height of the body: attribute inversely correlated with high hydrodynamic environments and directly correlated with the ability to develop vertical displacements (Gatz 1979a). Relative length of the caudal peduncle (RLCP): long peduncles indicate good swimmers, including benthic fish that inhabit high hydrodynamic environments (Gatz 1979b, Watson and Balon 1984). Compression index of the caudal peduncle (CICP): compressed peduncles indicate slow swimming and low maneuverability (Gatz 1979b). Ventral flattening index (VFI): fish with low values are associated with running water (Gatz 1979a). Relative area of the pectoral fin (RAPtF): high values are found in slow swimmers, or in individuals that use their flippers to attach themselves to the substrate (Watson and Balon 1984). Aspect ratio of the pectoral fin (ARPtF): high values indicate long and narrow fins, present in fishes that migrate large distances. Relative area of the caudal fin (RACdF): large caudal fins indicate movements in rapid pulses, a typical mode of swimming of several benthic fish (Watson and Balon 1984). Aspect ratio of the caudal fin (ARCdF): high values indicate active and continuous swimmers. Relative length of the pelvic fin (RLPlF): it is correlated with habitat preference, being longer in species that inhabit rocky habitats and shorter in nectonic species (Gatz 1979b). Relative length of the head (RLH): high values may indicate fish capable of preying on large prey (Gatz 1979b). Relative position of the eyes (RPE): benthic fish have dorsally located eyes, while nectones have lateral eyes (Watson and Balon 1984).

In order to test hypothesis two, the distribution of the individuals of each species in the morphological space was described through Principal Component Analysis (PCA), for which axes with eigenvalues greater than one were retained for interpretation. The differences in the morphometric variables between the two species were tested through Discriminant Analysis (AD).

To test which ecomorphological variables are correlated with the differences in the swimming capacity between the two species we applied a multiple regression between the morphological variables that differentiate them and the residuals of the regression between the critical velocity ($m \times s^{-1}$) and the standard length (cm). This approach was used to understand which morphological attributes besides size (standard length) are linked with the swimming capacity of both species of *Characidium*.

RESULTS

A significant difference was observed in the relative velocity measured from lengths per second between individuals of both species. Higher velocities (swimming capacity) were registered for *Characidum fasciatum* (14.51 lengths × s^{-1}; Min: 5.24 lengths × s^{-1}; Max: 24.86 lengths × s^{-1}; Std. Dev: 4.97) than for *C.* cf. *zebra* (12.78 lengths × s^{-1}; Min: 6.11 lengths × s^{-1}; Max: 15.69 lengths × s^{-1}; Std.Dev: 2.44) (Fig. 2). Body size (standard length) was positively correlated with the ability of both species to resist flow ($p < 0, 01$; $R^2 = 0.1543$; $F(1.42) = 7.66$) (Fig. 3).

The variables that presented higher values of loadings were RLH in the first main component axis, RACdF in the second axis and CICP, CI and RAPtF respectively third, fourth and fifth axis (Table 1). The Discriminant Analysis confirmed that the species differ significantly in the ecomorphological space, VFI (Ventral Flattening Index), RAPtF (Relative area of the pectoral flank), ARCdF (Aspect ratio of the caudal fin), RACdF (Relative area of the caudal fin) being the attributes that have the greatest influence on the distinction between the ecomorphological space of the two species (Table 2). Overall, specimens of *C. fasciatum* have dorso-ventrally flattened bodies and pectoral fins longer and narrower than *C.* cf. *zebra* specimens, which have in turn have longer caudal fin than *C. fasciatum* specimens (Fig. 4).

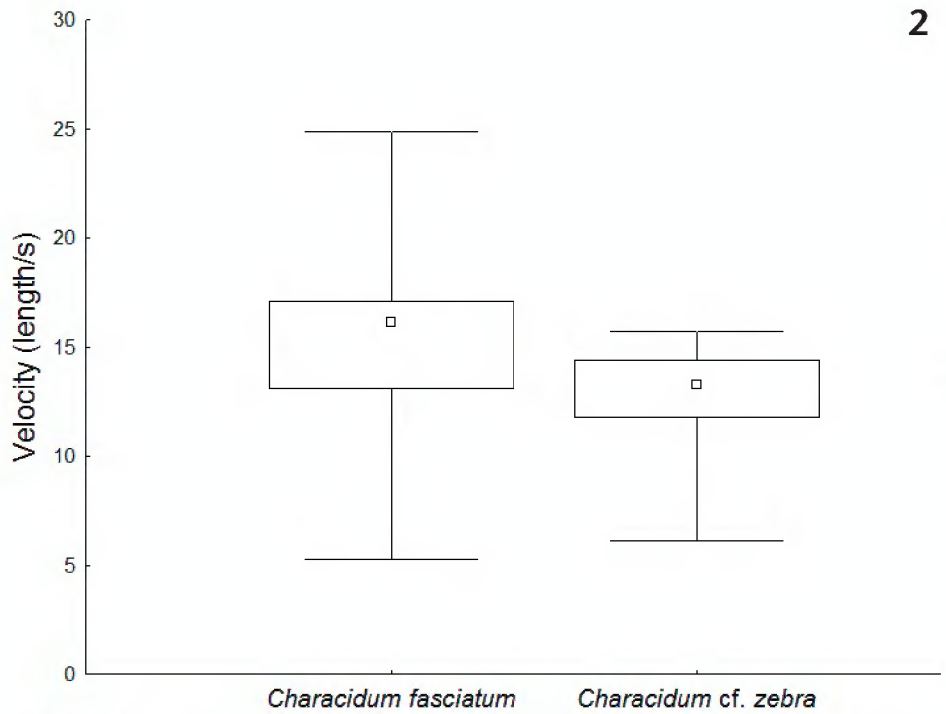
The multiple regression between the residuals of the regression between the critical velocity (m × s^{-1}) and the standard length (cm) and the attributes responsible for the differences in ecomorphological space between each species showed that the relative area of the pectoral fin (RAPtF) explained 18.22% of the velocity variation not explained by the individuals length [$(N = 44)$, $p < 0,05$, $R^2 = 0,2110$, R^2 adjusted= 0,1301, $F(4,39) = 2,60$] (Fig. 5).

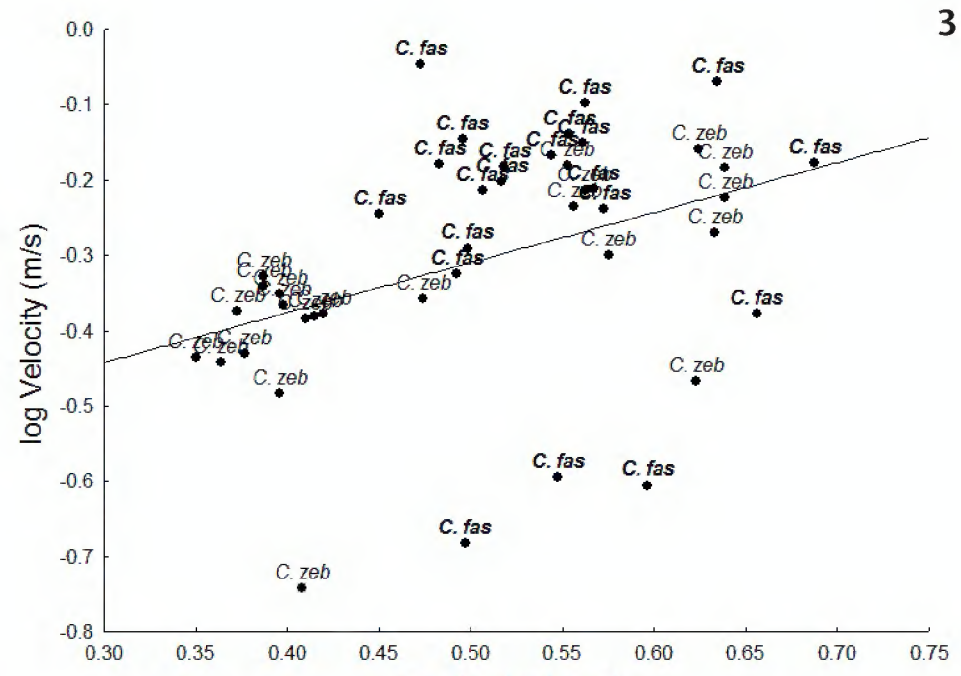
Table 1. Loadings of morphological variables on the first five axes of the Principal Component Analysis (eigenvalues > 1). The largest loadings are in bold.

Variables	CP 1	CP 2	CP 3	CP 4	CP 5
Compression index	0.101484	-0.649211	-0.067907	-0.647471	0.114110
Relative height of the body	-0.691127	-0.311125	-0.153900	-0.467784	0.259948
Relative length of the caudal peduncle	-0.627747	-0.269907	-0.215896	0.193572	-0.337416
Compression index of the caudal peduncle	0.386208	-0.318804	-0.713224	0.020561	-0.073561
Ventral flattening index	0.725761	-0.236215	-0.377391	0.223592	-0.360032
Relative area of the pectoral fin	-0.198724	0.385319	-0.241431	-0.548519	-0.542447
Aspect ratio of the pectoral fin	0.550045	-0.347654	-0.231541	0.164059	0.465828
Relative area of the caudal fin	-0.239776	0.837387	-0.322203	0.033375	0.146540
Aspect ratio of the caudal fin	-0.199099	-0.561589	0.580385	0.174781	-0.384017
Relative position of the eyes	0.705933	0.030894	-0.205489	-0.103314	-0.200997
Relative length of the head	-0.826480	-0.177116	-0.416453	0.134497	-0.002857
Relative length of the pelvic fin	-0.719176	-0.228822	-0.323839	0.387447	0.027592
Eigenvalues	3.695705	2.119175	1.599111	1.264256	1.050834
Explained variance (%)	30.79754	17.65979	13.32593	10.53547	8.75695
Cumulative variance (%)		48.4573	61.7833	72.3187	81.0757

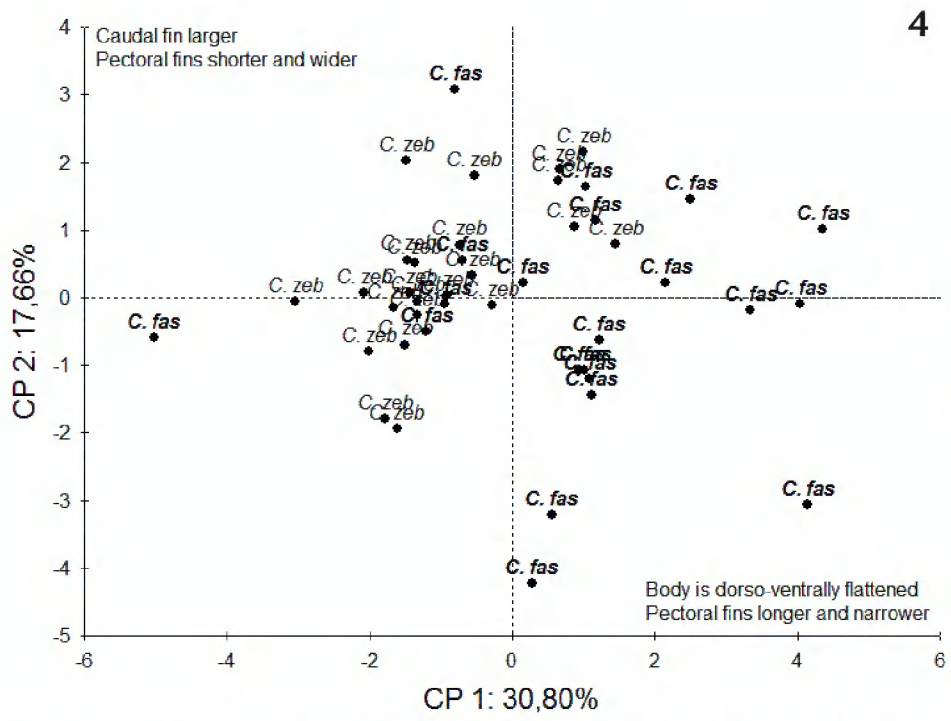
Table 2. Discriminant analysis of the ecomorphological attributes. The attributes in bold were the ones that best contributed to the ecomorphological difference ($F(12, 41) = 9.3160$ $p < 0.0000$).

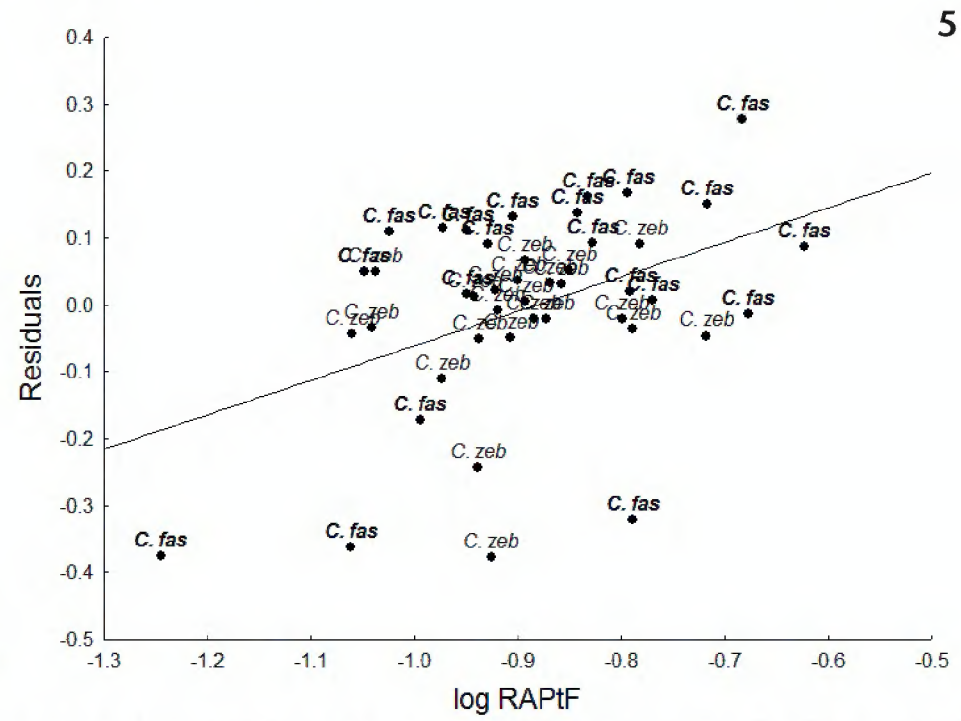
Ecomorphological Attribute	p	Wilks'- Lambda	Partial- Lambda	F-remove - (1,32)	Toler.
CI	0.238525	0.228040	0.955480	1.44443	0.460817
RH	0.815095	0.218278	0.998209	0.05563	0.196451
RLCP	0.051774	0.246651	0.883382	4.09240	0.460462
CICP	0.198019	0.230049	0.947134	1.73031	0.409357
VFI	0.002796	0.292016	0.746149	10.54664	0.235527
RAPtF	0.007493	0.275428	0.791086	8.18664	0.493864
ARPtF	0.817095	0.218270	0.998248	0.05441	0.568743
RACdF	0.003016	0.290697	0.749533	10.35908	0.245352
ARCdF	0.000485	0.324688	0.671067	15.19511	0.274885
RPE	0.928573	0.217945	0.999737	0.00817	0.620614
RLH	0.780003	0.218445	0.997446	0.07939	0.186914
RLPlF	0.263749	0.226993	0.959885	1.29555	0.317586





Figures 2–3. (2) Comparison between the relative velocities (length . s^{-1}) obtained for each species of *Characidium* in the tests of swimming capacity. Middle point represents Median, Box value are the percentiles and the Whisker-value is minimum and maximum values. (3) Relation between standard length (cm) and velocity ($m.s^{-1}$) for *Characidium fasciatum* (C.fas) and *Characidium* cf. *zebra* (C.zeb) species.





Figures 4–5. (4) Projection of the first two axes of Principal Component Analysis (PCA) for the two species *Characidium fasciatum* and *Characidium* cf. *zebra*. (5) Relationship between RAPtF (Relative area of the pectoral fin) and the regression residuals between standard length (cm) and velocity (m/s) for both species *Characidium fasciatum* (C.fas) and *Characidium* cf. *zebra* (C.zeb).

DISCUSSION

Our data show that *C. fasciatum* and *C.* cf. *zebra* have different swimming capacity and differ in the ecomorphological space. Collectively, our results support the three hypotheses tested. First, the species that thrive in the environment with greater hydrodynamism (*C. fasciatum*) has greater capacity to withstand the flow of water. Second, four ecomorphological attributes account for the differences between both species in the ecomorphological space. Third, swimming capacity is correlated with the morphological characteristics (pectoral fin morphology) and the swimming activity of the fish or with the capacity the fish has to resist the water flow by adhering to the substrate.

Characidium fasciatum has the greatest capacity to withstand the water flow. This allows them to inhabit areas where the water velocity is higher, as documented in a previous study of the habitat use and morphology of these species (Leal et al. 2011). Differences in swimming capacity between individuals are easy to observe when comparing species with different swimming styles, position in the water column or different preferences for substrates (Castro et al. 2010, Santos et al. 2012). Therefore, the information on the differences between individuals of the same species or congeneric species can give insights on species diversification.

Several studies, both in the northern and southern hemispheres, have showed a strong positive correlation between

swimming capacity and body size, often higher than 40% (Brett 1964, Jones et al. 1974, Santos et al. 2007, Castro et al. 2010, Srean et al. 2017). Most of these studies were carried out on species that travel long distances to reproduce. Body size, in these cases, is important not only for fish locomotion but also for their reproductive success. Body size is particularly important for the maintenance of energy reserves. However, a strong correlation between body size and swimming capacity can be found even in some small fish species (Sampaio 2009, Sampaio et al.2012, Castro et al. 2010, Srean et al. 2017). This includes species that also stand still on the substrate, and can be found in Trichomycteridae and Loricariidae (Burguess 1989). Nevertheless, the correlation between the capacity to support the flow of water and body size was not strong in the species analyzed in this study, which can be explained by their style of swimming. Species of *Characidium* spend much of their time positioned on the substrate using their pectoral fins, and actively swim mostly when they are looking for food (Casatti et al. 2001, Casatti and Castro 2006). This example shows that the relationship between swimming capacity and body size is not standard for all species.

In this study, we identified significant differences between some ecomorphological attributes of *C. fasciatum* and *C.* cf. *zebra*, possibly correlated with their differential use of the habitat. The attributes are responsible for the morphological distinction between the two species and are mainly in the swimming movement and/or the capacity to support water flow, such as ventral flattening index and relative area of the pectoral fin (Gatz 1979a, Watson and Balon 1984). The discriminant analysis also indicated that the relative area of the caudal fin and aspect ratio of the caudal fin were responsible for the morphological distinction between the two species. These two ecomorphological attributes are also linked to the capacity to perform active and fast movements. Therefore, the different flow velocity in the natural environment faced by the two studied species are strongly correlated with their morphology differences.

We provide information on the relationship between swimming capacity and morphological aspects, possibly correlated with the differential habitat use by two *Characidium* species. The studied species are found in drainages at the Brazilian savanna biome (also known as Cerrado), a global biodiversity hotspot (Myers et al. 2000) where agriculture is fast growing. Such land use change often jeopardizes streams by causing sedimentation, a contribution of fine sediment above the carrying capacity of the watercourse (Chapman et al. 2014). The deposition of sediment acts directly on the instream habitats by reducing both depth and substrate variability, homogenizing the streambed. Therefore, understanding the relationship between swimming capacity, morphology and habitat use may be important for identifying species that are prone to extinction by silting processes.

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